Energy requirements and metabolism of the Phillip's dikdik (Madoqua saltiana phillipsi)

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Abstract: Basal metabolic rates in mammals are mainly determined by body mass, but also by ecological factors. Some mammalian species inhabiting hot, dry environments were found to have lower metabolic rates compared to temperate species. We studied energy metabolism in Phillip's dikdik (Madoqua saltiana phillipsi), a small antelope inhabiting xeric shrubland habitats in the Eastern 'horn' of Africa, and compared results to literature data. We measured body mass (BM) changes and digestibility in 12 adults kept on different food intake levels to determine, by extrapolation to zero BM change, maintenance energy requirements (MEm) for metabolizable energy (ME). The MEm averaged at 404 ± 20 kJ ME kg BM -0.75 d-1. In addition we conducted 24 h-chamber respirometry with seven fed (non-fasted) individuals. Their mean metabolic rate as calculated from oxygen consumption was 403 ± 51 kJ kg BM-0.75 d-1, corroborating the results of the feeding trials. Selecting the 20 lowest values of the respiration measurement period to estimate resting metabolic rate (RMR) resulted in a mean RMR of 244 ± 39 kJ kg BM-0.75 d-1, which was numerically (but not significantly) lower than the expected basal metabolic rate of 293 kJ kg BM-0.75 d-1. Therefore, resting metabolism was similar to the expected average basal metabolism of a mammal of this size, which suggests a comparatively low metabolic rate in dikdiks. Compared to literature data Phillip's dikdiks have a MEm similar to measurements reported for small domestic ruminants, but considerably lower than those reported for other wild ruminant species inhabiting temperate and cold climates.

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A B S T R A C T

Basal metabolic rates in mammals are mainly determined by body mass, but also by ecological factors. Some mammalian species inhabiting hot, dry environments were found to have lower metabolic rates compared to temperate species. We studied energy metabolism in Phillip's dikdik (*Madoqua saltiana phillipsi*), a small antelope inhabiting xeric shrubland habitats in the Eastern 'horn' of Africa, and compared results to literature data. We measured body mass (BM) changes and digestibility in 12 adults kept on different food intake levels to determine, by extrapolation to zero BM change, maintenance energy requirements (MEm) for metabolizable energy (ME). The MEm averaged at 404 ± 20 kJ ME kg BM $^{-0.75}$ d^{-1}. In addition we conducted 24 h-chamber respirometry with seven fed (non-fasted) individuals. Their mean metabolic rate as calculated from oxygen consumption was 403 ± 51 kJ kg $BM^{-0.75}$ d^{-1}, corroborating the results of the feeding trials. Selecting the 20 lowest values of the respiration measurement period to estimate resting metabolic rate (RMR) resulted in a mean RMR of 244 ± 39 kJ kg $BM^{-0.75}$ d^{-1}, which was numerically (but not significantly) lower than the expected basal metabolic rate of 293 kJ kg $BM^{-0.75}$ d^{-1}. Therefore, *resting* metabolism was similar to the expected average *basal* metabolism of a mammal of this size, which suggests a comparatively low metabolic rate in dikdiks. Compared to literature data Phillip's dikdiks have a MEm similar to measurements reported for small domestic ruminants, but considerably lower than those reported for other wild ruminant species inhabiting temperate and cold climates.

Keywords:

Metabolism, dikdik, *Madoqua*, energy, respiration, maintenance requirements, resting metabolic rate, arid

1. Introduction

The basal metabolic rate (BMR) of mammals is mainly influenced by body mass (BM) (Kleiber, 1932; Brody, 1945; McNab, 2008), even though the exact scaling exponent of this allometric relationship has been the subject of intensive discussion (Glazier, 2005; Müller et al., 2012). However, it was repeatedly shown that there are other important factors besides BM influencing BMR such as habitat, climate, phylogeny, feeding habits or reproductive strategies, which explain some of the occasional deviation from the regression based on BM alone (e.g. McNab, 2008, Müller et al., 2012). Although Scholander et al. (1950) stated that animals do not adapt metabolic rate to climate, in particular McNab (2008) found that polar and cold-temperate habitats are inhabited by species with comparably high metabolic rates. Other studies demonstrated a lower metabolic rate in some mammals from hot environments when compared to species living in cold regions (as shown for an extensive dataset by Lovegrove, 2000, for canids in Careau et al., 2007, or small mammals in Lovegrove, 2003). Having a low metabolic rate in hot and/or arid environments can have several advantages: (1) it reduces endogenous heat load and thereby (2) reduces water loss for evaporative cooling (panting, sweating), which is the only physiological means for mammals to cool themselves (von Engelhardt and Breves, 2009); (3) it reduces energy requirements for maintenance, which is an important aspect in habitats that are not only characterized by drought but also where food can be limiting (Lovegrove, 2000). Overall, we can expect mammalian species living in hot, arid environments to have lower metabolic rates and energy requirements compared with species inhabiting regions with temperate climates.

In ruminants, dikdiks (*Madoqua* spp.), amongst the smallest extant species, have been labeled a miniature model for comparative physiological investigations (Maloiy et al., 1988). These animals inhabit the dry bush country of eastern and southern Africa, where conditions are semi-arid to arid, ambient temperatures are typically high, and surface water availability is low (Hendrichs and Hendrichs, 1971; Maloiy, 1973). During the dry season, dikdiks are

additionally forced to cope with food scarcity (Manser and Brotherton, 1995). Several studies have already used dikdiks to study organismal adaptations, such as thermoregulation and water metabolism, to these harsh environmental conditions (Maloiy, 1973; Maskrey and Hoppe, 1979; Kamau and Maloiy, 1985; Kamau, 1988). However, results have been inconsistent across studies, and therefore generalized conclusions are difficult to make. For instance, a mammal of dikdik size is expected to have a metabolic rate around 293 kJ kg $BM^{-0.75}$ d^{-1} (based on the equation of Kleiber, 1961; see Methods), but values above and below this level have been reported. Maskrey and Hoppe (1979), using flow-through face masks, found a 20% higher-than-expected metabolic rate of 354 kJ kg $BM^{-0.75}$ d^{-1} in Kirk's dikdik (*M. kirkii*), which they ascribed to the fact that subjects were not in a basal, post-absorptive condition during measurement. Another explanation could be that the high metabolic rates reflected a response to stress because the respiratory measurements had been carried out using face-masks. Applying chamber respirometry, Kamau and Maloiy (1981) found relatively low fasting metabolic rates of 154 to 218 kJ kg $BM^{-0.75}$ d^{-1}, and suggested that this was an adaptation to heat and aridity. High metabolic rates have also been reported by Hoppe (1983) (374 kJ kg $BM^{-0.75}$ d^{-1} in fasting, and 406 ± 17 kJ kg $BM^{-0.75}$ d^{-1} in fed, animals respectively), and low rates of 168 (dehydrated, fed individuals) to 223 kJ kg $BM^{-0.75}$ d^{-1} (hydrated, fed individuals) were shown again by Kamau and Maloiy (1983). The most recent finding of 296 kJ kg $BM^{-0.75}$ d^{-1} (Kamau, 1988) is close to the expected mammal average. This illustrates a huge between-study variation, which might at least partly be a consequence of the differences between the methods applied.

The disparity in published data for dikdik metabolic rates has resulted in inconsistent inclusion of this species in broader-scale comparative studies. Špála et al. (1987) used the results of Kamau and Maloiy (1981) in a comparative dataset to investigate energy requirements of domestic and captive wild ruminants. In that instance, the dikdik had an extraordinarily low value, which the authors had interpreted as a special adaptation to hot arid

environments. In the comparative data collection of Lovegrove (2000), (which was later also used by Savage et al., 2004), an average value from the studies of Maskrey and Hoppe (1979) and Kamau and Maloiy (1982) was used, with a classification of the dikdik as a species inhabiting mesic rather than desert environments. Using this average, the dikdik's metabolism would be very close to the general mammalian average. In contrast, in the data collection of McNab (2008), only the data of Kamau (1988) were used, with a classification of the dikdik as inhabiting xeric environments. Although disparate categorization of a single species is unlikely to influence the overall result of these comparative studies which comprise data for large numbers of taxa - both Lovegrove (2000) and McNab (2008) – the question whether or not dikdiks show dry-region adaptations in their metabolic rate remains unsolved.

In order to clarify this controversy, we (i) evaluated the relationship between digestible energy intake and BM change as a means to estimate maintenance energy requirements (MEm), using data from a completed experiment in captive Phillip's dikdik (Hebel et al. 2011), and (ii) conducted individual gas exchange measurements in transportable respiratory chambers for the determination of metabolic rates. For comparison, we carried out a literature review on energy requirements in ruminants.

2. Materials and Methods

The two experiments were conducted at Al Wabra Wildlife Preservation (AWWP), Qatar, with adult Phillip's dikdiks (*Madoqua saltiana phillipsi*) (hereafter referred to as dikdiks). Prior to the experiments, the animals were housed and fed according to AWWP guidelines for dikdik husbandry (Hammer, 2009). The animals were monitored constantly by a veterinarian, and subsequently released into their original pens after the experiments.

2.1. Measurement of maintenance energy requirements (Experiment 1)

In experiment 1, 12 dikdiks (ten males, two females, mean initial body mass 2.36 ± 0.23 kg) were housed in separate indoor pens (2.4 × 1.5 × 2.5 m) without visual contact to their neighbors. The pens were supplied with cat carriers and cardboard plates as shelters as well as a rubber mat, which the animals accepted as a spot for defecation. Water and food were offered in separate stainless steel bowls and pens were cleaned on a daily basis. Artificial light was provided between 06:00 and 18:00 inside the pens and temperatures were maintained between 19 and 25 °C. All animals underwent an initial adaptation period of one week to become accustomed to the pens and the researcher.

All individuals experienced three treatment phases where they received food on different intake levels: *ad libitum*, 85% of the individual's previous *ad libitum* intake, and 70% of the *ad libitum* intake. Each treatment phase consisted of a two-week adaptation period followed by a one-week collection period. The *ad libitum* treatment was performed by offering unrestricted access to two types of pellets (Table 1). In addition to the pellets, each animal received between 45 and 60 g of fresh alfalfa (*Medicago sativa*) leaves daily, which were removed from their stalks by hand, and 14 g of a grated mix of carrots and apple mixed with 1 g wheat bran (see Table 1 for nutrient composition). The animals received fresh food every morning. Every day, food samples were taken and the animals were weighed daily. In order to determine the intake of digestible energy, both feces and food refusals were completely collected during the collection periods for later analyses (controlling for exsiccation by a separate food sample exposed to the same environmental conditions as the food provided). More details on the experiment can be obtained from Hebel et al. (2011).

All samples were air dried at about 50°C immediately after sampling, and ground to 0.75 mm with a mill (Retsch GmbH, Haan, Germany). Foods, refusals and feces were analyzed for dry matter content by drying at 103°C to constant weight. Gross energy (GE) was determined by bomb calorimetry (IKA-Kalorimeter C4000, Ika, Stauffen, Germany). Total ash was analyzed as outlined in Naumann and Bassler (1976) in a muffle furnace, and the difference

153 from dry matter was considered as organic matter. For determinations of nitrogen (N) by the
154 Dumas method, an Elementar rapid N III Analyzer (Elementar Analysensysteme, Hanau,
155 Germany) was used. Crude protein (CP) was calculated as 6.25 × N. Neutral detergent fiber
156 (NDF; after treatment with α-amylase) and acid detergent fiber (ADF) were analyzed as
157 described previously (Van Soest, 1967; Van Soest et al., 1991) using the Ankom200 Fiber
158 Analyzer. The fiber data were corrected for ash content.

159 Using intakes and fecal losses of energy as well as BM, the daily intake of digestible
160 energy (in kJ kg $BM^{-0.75}$ d^{-1}) was computed for each animal. Metabolizable energy (ME) was
161 calculated as digestible energy (DE) × 0.82 (NRC, 1984). The average body mass change
162 measured during the collection period was calculated as the percentage of BM change per day
163 in relation to BM measured at the beginning of each treatment period. To estimate MEm from
164 these data, we applied a linear mixed model with daily BM change as the dependent and daily
165 ME intake (MEi) as the independent variable, including individual as a random factor. Based
166 on the resulting regression, MEm was determined as the MEi where there was zero BM
167 change. Analyses were carried out with R 2.15.0 using the package nlme (Pinheiro et al.,
168 2007). In addition to the experiment, a literature research on MEm values of other ruminant
169 species was carried out to allow a comparative interpretation of the values obtained in the
170 present study.

171

172 *2.2. Measurements of metabolic rate in respiratory chambers (Experiment 2)*

173 Measuring body mass changes to determine energy requirements without simultaneously
174 monitoring body composition bears the risk that the use of adipose tissue (which is replaced
175 by water) is not detected, and that the consistency in weight is interpreted as a balanced
176 energy turnover (Kirchgessner, 2011). Therefore, we additionally performed respiration
177 measurements.

178 In Experiment 2, seven individual dikdiks (mean body mass 2.00 ± 0.15 kg) were kept
179 with *ad libitum* access to a diet of fresh alfalfa (see Table 1 for nutrient composition) and
180 water in 2.4 × 1.0 m pens for 3 weeks prior to the measurements. Dry matter intake was
181 determined for one week prior to the measurements, averaging 31 ± 4 g kg $BM^{-0.75}$ d^{-1} per
182 individual. Temperatures were held at ~25°C which ensured that the subjects were under
183 thermoneutral conditions (Kaumau, 1988, reported a thermoneutral zone of 24 – 35°C for
184 Kirk's dikdiks). The subjects were then put separately for 24 h into one of three airtight
185 wooden transport-type boxes (1.0 × 0.7 × 0.6 m) used as respiration chambers. There, a carpet
186 of woodchips and fresh alfalfa (in amounts exceeding the previously recorded *ad libitum*
187 intake) were provided. Chambers were fitted with air inlets on the bottom and air outlets on
188 top of the box to ensure a constant airflow (10 to 15 l min^{-1}) generated by a pump (Flowkit
189 100, Sable Systems, Las Vegas, USA). Out-flowing air was ducted via flexible hoses to a gas
190 multiplexer, which allowed the measurement of data on three individuals and baseline values
191 from ambient air simultaneously, at alternating intervals of 120 to 180 seconds each. Gas
192 concentrations were measured by O_2 and CO_2 analyzers (Turbofox, Sable Systems). Data
193 were adjusted for barometric pressure, water vapor pressure and air flow rates, which were
194 constantly recorded during respirometry. The gas analyzers were calibrated prior to each
195 measurement by using pure nitrogen and a span gas (PanGas, 20% O_2 and 1% CO_2 dissolved
196 in nitrogen). Data obtained by the respiratory system were analyzed with the software
197 ExpeData (Sable Systems) for O_2 consumed and CO_2 emitted after correcting for gas
198 concentrations in ingoing air. The mean metabolic rate was calculated based on the entire
199 measurement and therefore accounts for the activity of the animals inside the box (e.g.
200 walking around and feeding), while the resting metabolic rate (RMR) of the animals was
201 determined by selecting the 20 lowest O_2 measurements per individual within the 24-h period
202 (adapted from Derno et al. 2005). In order to calculate MR we multiplied the amount of O_2
203 consumed (in l h^{-1}) by 20.08 kJ (McNab, 2008).

To compare the MR of our animals to their expected BMR, we used the equation of Kleiber (1961), which yielded and expected BMR of 293 kJ × kg $BM^{-0.75}$. This equation uses a scaling exponent of 0.75, which has been confirmed to be appropriate for artiodactyls by McNab (2008). The values of our measurements were tested for normal distribution and then statistically compared with the expected values by applying a Mann-Whitney-U test in R 2.15.0.

3. Results

In Experiment 1, out of the 12 individuals used in this study, 3 animals did not gain weight on any of the treatments used, i.e., not even when feed was offered *ad libitum*. For animal welfare reasons, the experimental period with an intake level of 70% had to be replaced by a second *ad libitum* session in two individuals. The regression equation determined based on the mixed model (BM change = 0.0016 (± 0.0004) × MEi - 0.64 (± 0.13), n = 12) resulted in a MEm of 404 ± 20 kJ kg $BM^{-0.75}$ d^{-1} for our subjects (Fig. 1).

In Experiment 2, O_2 consumption and CO_2 production fluctuated throughout the 24 h of measurement, indicating the presence of different phases of activity (and potentially also endogenous circadian rhythms). O_2 consumption was highest during daytime, decreasing through the night (Fig. 2). However, small peaks in O_2 consumption and CO_2 production indicate that regular phases of activity still occurred at night, which were accompanied by an elevated respiratory quotient (RQ) indicating a relatively higher CO_2 production. The mean metabolic rate of the animals was 403 ± 51 kJ kg $BM^{-0.75}$ d^{-1}. Selecting the lowest 20 O_2 measurements led to a mean RMR of 244 ± 39 kJ kg $BM^{-0.75}$ d^{-1}, a value that is lower than the expected 293 kJ kg $BM^{-0.75}$ d^{-1}. However, this difference was not significant when we compared the measured RMR and the estimated BMR of each individual (n = 7, U = 19, p = 0.47) (Fig. 3).

4. Discussion

Comparing the MEm values for dikdiks from the present study, as measured by feeding trials and respiration measurements, with literature data for other selected species (Table 2) reveals that the dikdik is located at the lower end of the range in MEm covered by the ruminant species for which data exist. However, the dataset includes only few species that can be classified as inhabiting tropical environments (e.g, the mouse deer). This impedes the comparison among species. Additionally, the literature data comprises a number of domesticated species, which have often been intensively selected for high productivity rather than for low MEm. Nevertheless, the low MEm values obtained in the present study are remarkable, as it has to be considered that the experiments were carried out with non-domestic animals not used to regular handling. Our subjects seemed to cope well with the daily disturbance caused by humans, but it still cannot be excluded that the animals exhibited higher levels of stress, associated with elevated MEm, during the experiments than one would expect in domestic ruminants or in undisturbed free-ranging specimens.

The difference between expected (estimated) and measured RMR was not statistically significant. The way of estimation was based on the calculation of the basal metabolic rate, i.e. a post-absorptive, quiescent metabolic state at thermoneutral conditions (Schmidt-Nielsen, 1997). The problem of measuring basal metabolism in herbivores, having a fermentation chamber that will not be empty most of the time and thereby hardly ever allow a post-absorptive state to be achieved, was addressed by White and Seymour (2003). Additionally, in our respiratory chambers, the animals were able to move and eat. Due to these reasons we were only able to measure resting MR, even though we selected the 20 lowest values of the set of measurements. As RMR can be assumed to be higher than the BMR, the difference between expected and actual BMR in dikdiks can be assumed to be even larger. The dikdiks had a metabolic rate of 403 ± 51 kJ kg $BM^{-0.75}$ d^{-1} when averaged over the entire 24-h measurement. A similar measurement carried out with goats by Lachica et al. (1997) revealed

256 a heat production of 405 kJ kg $BM^{-0.75}$ d^{-1}, which is close to the value obtained in this study.
257 However, the measurements on goats were carried out 16 – 20 h after feeding which impedes
258 the comparison with our data; actually, if fasted goats have a similar energy turnover as fed
259 dikdiks, this supports the hypothesis that dikdiks have a comparatively low metabolism.

260 Together, our results on MEm and RMR qualitatively match the findings for some other
261 mammal groups that species inhabiting arid and hot regions have a lower metabolism when
262 compared to species living in cold environments. Regarding their energy requirements,
263 dikdiks, together with some (but not all) measurements in domestic sheep and goats, range at
264 the lower end of data in the ruminant spectrum. The available data on ruminants are
265 somewhat limited as they are based mainly on domestic species typically kept in temperate
266 regions. Comparing our results to those obtained in other African bovids (Table 3) shows that
267 the MR of the Phillip's dikdik indeed falls below the reported average values. The
268 observation that the Phillips dikdik has comparably low energy requirements and a
269 metabolism that is slightly lower than expected supports the findings of Kamau and Maloyi
270 (1981, 1983) in Kirk's dikdiks. These findings can be interpreted as adaptation to the harsh
271 environmental conditions of their natural habitat, i.e. scarcity of food, high temperatures and
272 low water availability. However, the fact that other ruminant species that are also exposed to
273 similar climatic challenges, like the Arabian oryx (*Oryx leucoryx)* or the goitered gazelle
274 (*Gazella subgutturosa*), do not share the characteristic of a comparatively low metabolism
275 (Table 3) also suggests that ruminants have a variety of physiological and behavioural
276 adaptations at their disposal (e.g. Ostrowski et al., 2003) that facilitates the use of different
277 habitats, and that a low metabolism is not a compulsory asset of species inhabiting xeric
278 niches. Given the low number of ruminant species for which such data are available, a
279 phylogeny-based analysis of variation in MR with habitat is not feasible.

280 A particular finding was that, during the 24-h measurement, periodical fluctuations in O_2
281 consumption and CO_2 production were observed. The high levels at the beginning of each 24-

h measurement were probably not only caused by diurnal activity of the animals but are also a reflection of stress as a response to the transfer into the respiration chambers. During the night, O_2 consumption and CO_2 production were generally reduced but interrupted by regular peaks accompanied with rises in RQ levels, which could reflect phases of rumination or eating and thereby the effect of the associated specific dynamic action (e.g. McClymont, 1952). Hoppe et al. (1983) reported alternating phases of eating and ruminating in dikdiks, lasting 1 to 36 min in the former and 1 to 38 min in the latter. However, the time between the peaks observed in our measurements ranged between 1 and 3 h, which could indicate that either the Phillip's dikdiks used in this study had a different feeding rhythm, or that these periods reflect activities independent of rumination and feeding.

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References

Aguilera, J.F., Molina, E., Prieto, C., Boza, J., 1986. Estimacion de las necesidades energeticas de mantenimiento en ganado ovino de raza segurena. Archivos de zootecnia 35, 89–96.

Baker, D.L., Johnson, D.E., Carpenter, L.H., Wallmo, O.C., Gill, R.B., 1979. Energy requirements of mule deer fawns in winter. J. Wildl. Manage. 43, 162-169.

Brody, S., 1945. Bioenergetics and Growth, with Special Reference to the Efficiency Complex in Domestic Animals. Reinhold Publishing Co., New York, USA.

Careau, V., Morand-Ferron, J., Thomas, D., 2007. Basal metabolic rate of Canidae from hot deserts to cold arctic climates. J. Mammal. 88, 394-400.

Darlis, Abdullah, N., Liang, J.B., Ho, Y.W., 2011. Energy requirement for maintenance of growing and adult male lesser mouse deer (*Tragulus javanicus*) in captivity. Mamm. Biol. 76, 365-368.

Derno, M., Jentsch, W., Schweigel, M., Kuhla, S., Metges, C.C., Matthes, H.D., 2005. Measurements of heat production for estimation of maintenance energy requirements of Hereford steers. J. Anim. Sci. 83, 2590-2597.

Ferrell, C., Jenkins, T., 1985. Cow type and the nutritional environment: nutritional aspects. J. Anim. Sci. 61, 725-741.

GfE (Gesellschaft für Ernährungsphysiologie), 1996. Energie-Bedarf von Schafen. Proc. Soc. Nutr. Physiol. 5, 149-152.

GfE (Gesellschaft für Ernährungsphysiologie), 2003. Recomendations for the Supply of Energy and Nutrients to Goats. DLG Verlag, Frankfurt, Germany.

Glazier, D.S., 2005. Beyond the ¾-power law: variation in the intra and interspecific scaling of metabolic rate in animals. Biol. Rev. 80, 611-662.

Hammer, C., 2009. Phillips Dikdiks (*Madoqua saltiana phillipsi*) in der Al Wabra Wildlife Preservation (AWWP) / Katar. Der Zoologische Garten 78, 265-281.

Hebel, C., Ortmann, S., Hammer, S., Hammer, C., Fritz, J., Hummel, J., Clauss, M., 2011. Solute and particle retention in the digestive tract of the Phillip's dikdik (*Madoqua saltiana phillipsi*), a very small browsing ruminant: Biological and methodological implications. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 159, 284-290.

Hendrichs, H., Hendrichs, U., 1971. Dikdik und Elefanten. R. Piper, München, Germany.

333 Hoppe, P.P., Van Hoven, W., von Engelhardt, W., Prins, R.A., Lankhorst, A., Gwynne, M.D.,
334 1983. Pregastric and caecal fermentation in dikdik (*Madoqua kirki*) and suni (*Nesotragus*
335 *moschatus*). Comp. Biochem. Physiol. A Physiol. 75, 517-524.
336 Kamau, J.M.Z., 1988. Metabolism and evaporative heat loss in the dik-dik antelope
337 (*Rhynchotragus kirki*). Comp. Biochem. Physiol. A Physiol. 89, 567-574.
338 Kamau, J., Maloiy, G., 1981. The fasting metabolism of a small East African antelope: the
339 dik-dik. J. Physiol. 319, 50-51.
340 Kamau, J.M.Z., Maloiy, G.M.O., 1982. The relationship between rate of oxygen
341 consumption, heart rate and thermal conductance of the dik-dik antelope (*Rhynchotragus*
342 *kirkii*) at various ambient temperatures. Comp. Biochem. Physiol. A Physiol. 73, 21-24.
343 Kamau, J., Maloiy, G., 1983. Changes in thyroxine, triiodothyronine and metabolic rate in the
344 dik-dik antelope (*Rhynchotragus kirkii*): effects of temperature and dehydration. J. Comp.
345 Physiol. 152, 23-26.
346 Kamau, J.M.Z., Maloiy, G.M.O., 1985. Thermoregulation and heat balance in the dik-dik
347 antelope *Rhynchotragus kirki*: A field and laboratory study. Comp. Biochem. Physiol. A
348 Physiol. 81, 335-340.
349 Kirchgessner, M., Roth, F.X., Schwarz, F.J., Stangl, G.I., 2011. Tierernährung. 13th ed., DLG
350 Verlag, Frankfurt, Germany.
351 Kleiber, M., 1932. Body size and metabolism. Hilgardia 6, 315-353.
352 Kleiber, M., 1961. The Fire of Life: An Introduction to Animal Energetics. John Wiley, New
353 York, USA.
354 Lachica, M., Prieto, C., Aguilera, J.F., 1997. The energy cost of walking on the level and on
355 negative and positive slopes in the Franadia goat (Capra hircus). Br. J. Nutr.77, 73-81.
356 Lachica, M., Aguilera, J., 2003. Estimation of energy needs in the free-ranging goat with
357 particular reference to the assessment of its energy expenditure by the ^{13}C-bicarbonate
358 method. Small Rumin. Res. 49, 303-318.

359 Lovegrove, B.G., 2000. The zoogeography of mammalian basal metabolic rate. Am. Nat. 156,
360 201-219.
361 Lovegrove, B.G., 2003. The influence of climate on the basal metabolic rate of small
362 mammals: a slow-fast metabolic continuum. J. Comp. Physiol. B 173, 87-112.
363 Luo, J., Goetsch, A.L., Sahlu, T., Nsahlai, I.V., Johnson, Z.B., Moore, J.E., Galyean, M.L.,
364 Owens, F.N., Ferrell, C.L., 2004. Prediction of metabolizable energy requirements for
365 maintenance and gain of preweaning, growing and mature goats. Small Rumin. Res. 53,
366 231-252.
367 Maloiy, G., 1973. The water metabolism of a small East African antelope: the dik-dik. Proc.
368 Biol. Sci. 184, 167-178.
369 Maloiy, G.M.O., Rugangazi, B.M., Clemens, E.T., 1988. Physiology of the dik-dik antelope.
370 Comp. Biochem. Physiol. A Physiol. 91, 1-8.
371 Manser, M., Brotherton, P., 1995. Environmental constraints on the foraging behaviour of a
372 dwarf antelope (*Madoqua kirkii*). Oecologia 102, 404-412.
373 Maskrey, M., Hoppe, P., 1979. Thermoregulation and oxygen consumption in Kirk's dik-dik
374 (*Madoqua kirkii*) at ambient temperatures of 10 – 45 °C. Comp. Biochem. Physiol. A
375 Physiol. 62, 827-830.
376 McClymont, G.L., 1952. Specific dynamic action of acetic acid and heat increment of feeding
377 in ruminants. Aust. J. Biol. Sci. 5, 374-384
378 McNab, B.K., 2008. An analysis of the factors that influence the level and scaling of
379 mammalian BMR. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 151, 5-28.
380 Müller, D.W., Codron, D., Werner, J., Fritz, J., Hummel, J., Griebeler, E.M., Clauss, M.,
381 2012. Dichotomy of eutherian reproduction and metabolism. Oikos 121, 102-115.
382 Naumann, C., Bassler, R., 1976. Die chemische Untersuchung von Futtermitteln. VDLUFA-
383 Verlag, Darmstadt, Germany.

National Research Council. 1984. Nutrient Requirements of Domestic Animals. No. 4. Nutrient Requirements of Beef Cattle. National Academy of Sciences, Washington DC.

National Research Council. 2007. Nutrient Requirements of Small Ruminants: Sheep, Goats, Cervids, and New World Camelids. The National Academies Press, Washington, DC.

Ostrowski, S., Williams, J. B., Ismael, K., 2003. Heterothermy and the water economy of free-living Arabian oryx (Oryx leucoryx). J. Exp. Biol. 206, 1471-1478.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2007. Linear and nonlinear mixed effects models. R package version 3, 57.

Prieto, C., Aguilera, J., Lara, L., Fonollá, J., 1990. Protein and energy requirements for maintenance of indigenous Granadina goats. Br. J. Nutr. 63, 155-163.

Renecker, L.A., Hudson, R.J., 1985. Estimation of dry matter intake of free-ranging moose. J. Wildl. Manage. 49, 785-792.

Savage, V.M., Gillooly, J., Woodruff, W., West, G., Allen, A., Enquist, B., Brown, J., 2004. The predominance of quarter-power scaling in biology. Funct. Ecol. 18, 257-282.

Schmidt-Nielsen, K., 1997. Animal Physiology: Adaptation and Environment. Cambridge University Press, New York, USA.

Scholander, P., Hock, R., Walters, V., Irving, L., 1950. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biol. Bull. 99, 259-271.

Schwartz, C.C., Hubbert, M.E., Franzmann, A.W., 1988. Energy requirements of adult moose for winter maintenance. J. Wildl. Manage. 52, 26-33.

Silanikove, N., 1986. Interrelationships between feed quality, digestibility, feed consumption, and energy requirements in desert (Bedouin) and temperate (Saanen) goats. J. Dairy Sci. 69, 2157-2162.

Solis, J., Byers, F., Schelling, G., Long, C., Greene, L., 1988. Maintenance requirements and energetic efficiency of cows of different breed types. J. Anim. Sci. 66, 764-773.

410 Špála, P., Špráchal, M., Hradecký, P., 1987. Physiological characteristics of mountain
411 reedbuck fed a controlled ration. J. Wildl. Manage. 51, 379-383.
412 Ullrey, D., Youatt, W., Johnson, H., Fay, L., Schoepke, B., Magee, W., 1970. Digestible and
413 metabolizable energy requirements for winter maintenance of Michigan white-tailed does.
414 J. Wildl. Manage. 34, 863-869.
415 Van Soest, P., 1967. Development of a comprehensive system of feed analyses and its
416 application to forages. J. Anim. Sci. 26, 119-128.
417 Van Soest, P., Robertson, J., Lewis, B., 1991. Methods for dietary fiber, neutral detergent
418 fiber, and nonstarch polysaccharides in relation to animal nutrition. J. Dairy Sci. 74, 3583-
419 3597.
420 Vermorel, M., Dulphy, J.P., Bouvier, J.C., 1987. Energy utilization of sodium hydroxide
421 treated or untreated straw supplemented with protein or concentrates by adult sheep. Arch.
422 Anim. Nutr. 37, 805-821
423 von Engelhardt, W., Breves, G., 2009. Physiologie der Haustiere. 3rd ed., Georg Thieme
424 Verlag, Stuttgart, Germany.
425 White, C.R., Seymour, R.S., 2003. Mammalian basal metabolic rate is proportional to body
426 mass$^{2/3}$. Proc. Nat. Acad. Sci. 100, 4046-4049.

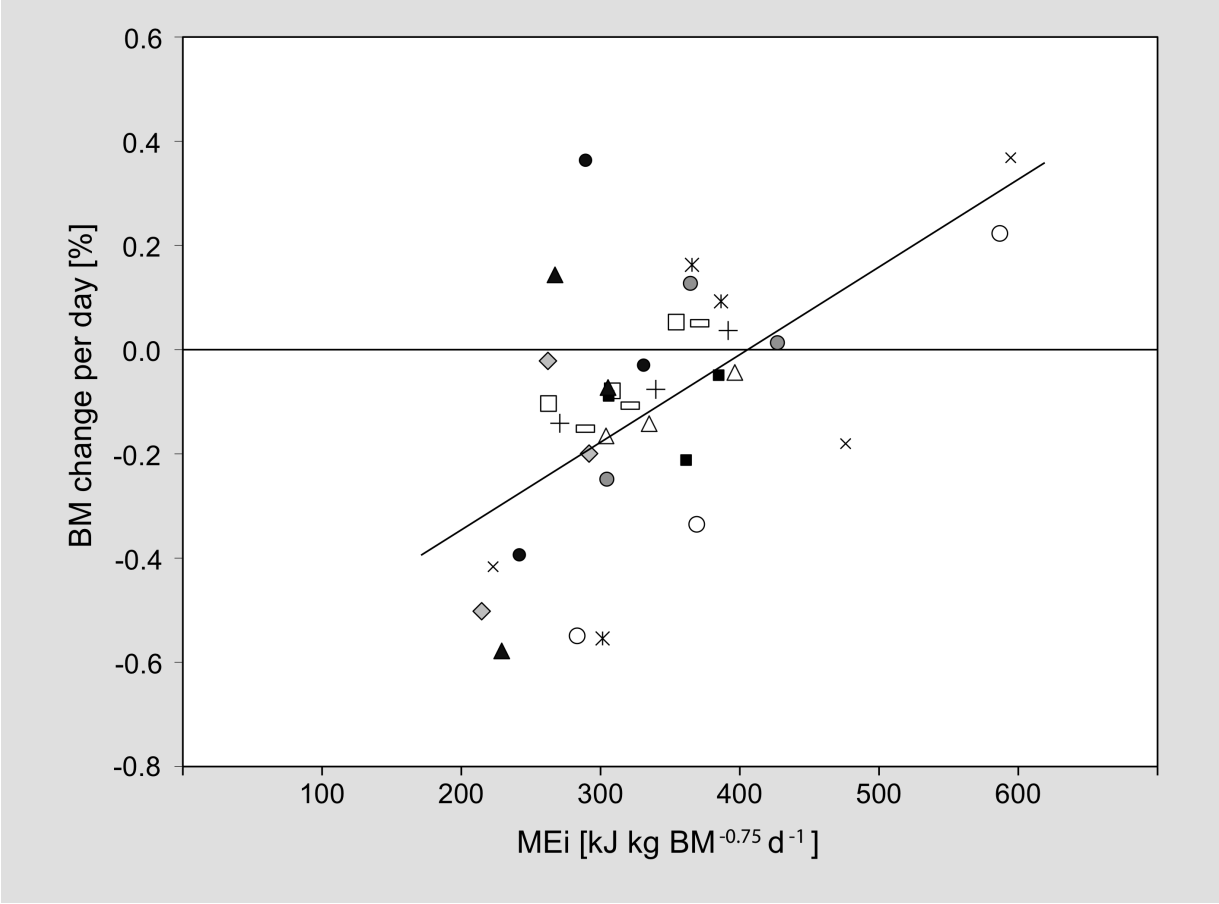

Fig. 1. Individual measurements in Experiment 1 and linear regression of body mass (BM) change in % of the initial weight (y) as a function of intake of metabolizable energy (MEi; x). The equation is y = 0.0016 x - 0.64. The MEi was calculated as 0.82 × digestible energy. Each symbol represents one individual at one of the three different intake levels.

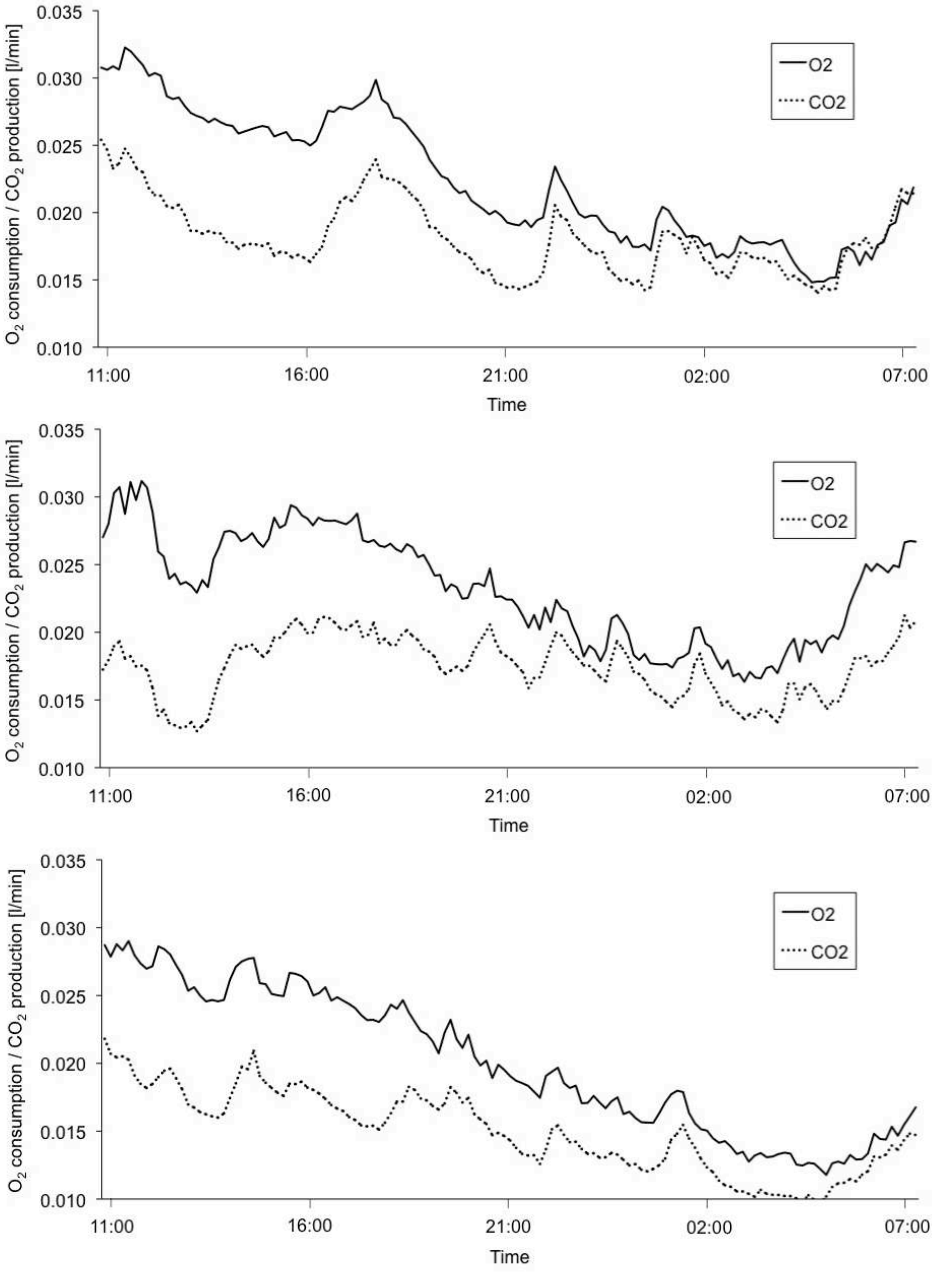

Fig. 2. Time course of O_2 consumption and CO_2 production of three exemplary individuals during 20 h of measurement in the respiration chambers during Experiment 2. Note the regular peaks interrupting the general decrease in both values during the night.

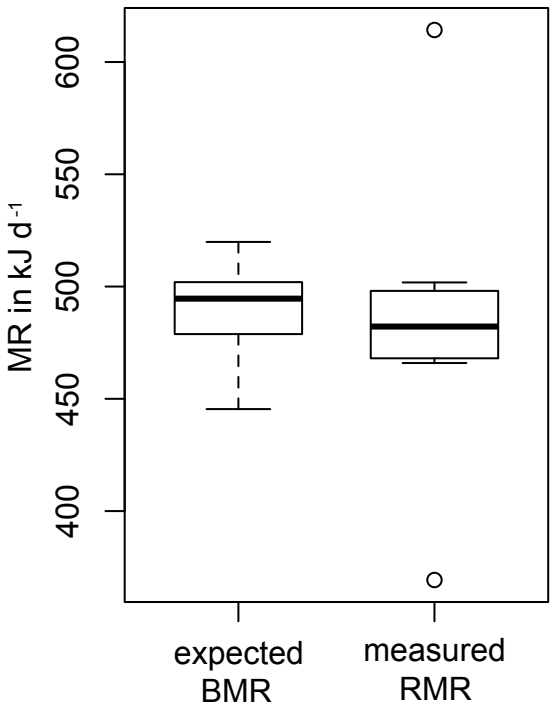

Fig. 3. Comparison of the measured resting metabolic rate (RMR) with the expected basal metabolic rate (BMR) for the individuals in Experiment 2 (U = 19, $p = 0.47$).

Table 1

Nutrient composition (g/kg dry matter) of the diet items offered during the experiments.

Food	Crude protein	Neutral detergent fiber	Acid detergent fiber	Ash
Experiment 1				
Carrot	62.0	109.2	80.8	75.8
Apple	19.0	78.0	52.8	14.8
Pellets (Mazuri)[a]	169.0	392.9	186.6	84.4
Pellets (Altromin)[b]	198.3	335.5	187.6	92.7
Wheat bran	163.3	440.0	134.3	51.7
Alfalfa leaves	280.4	210.3	125.6	162.5
Experiment 2				
Alfalfa leaves	296.3	203.4	149.5	187.0

[a] Composed of wheat, wheat feed, soy bean meal, soy bean hulls, soy bean oil, glucose, molasses, grass meal, cellulose powder, vitamin premix, and mineral premix; produced by Mazuri Zoo Foods (Altrip, Germany), Browser Maintenance.

[b] Composed of wheat bran, grass meal, wheat feed, soy bean meal, soy bean hulls, calcium carbonate, sodium chloride, vitamin premix, and mineral premix; produced by Altromin Spezialfutter GmbH & Co. KG (Lippe, Germany), Breeding Maintenance Diet for small ruminants.

Table 2

Maintenance requirements for metabolizable energy (MEm) of ruminant species as reported in the literature and ordered by MEm.

Species	Common name	MEm (kJ kg $BM^{-0.75}$ d^{-1})	Reference
Odocoileus hemionus	Mule deer	661	Baker et al. (1979)
Odocoileus virginianus	White tailed deer	661	Ullrey et al. (1970)
Capra hircus	Goat (cold environment)	641	Silanikove (1986)
Alces alces	Moose	584	Renecker and Hudson (1985)
Rangifer tarandus	Caribou	572-766	NRC (2007)
Odocoileus virginianus	White tailed deer	565-724	NRC (2007)
Alces alces	Moose	548	Schwartz et al. (1988)
Cervus elaphus	Red deer	544-850	NRC (2007)
Rangifer tarandus	Reindeer	494-607	NRC (2007)
Capra hircus	Goat	462 - 489	NRC (2007)
Capra hircus	Goat	450	GfE (2003)
Capra hircus	Goat	443	Prieto et al. (1990)
Tragulus javanicus	Mouse deer	436	Darlis et al. (2011)
Capra hircus	Goat	431	Luo et al. (2004)
Capra hircus	Sheep	430	GfE (1996)
Bos taurus	Cattle	427 - 674	Ferrell and Jenkins (1985)
Bos taurus	Cattle	426	Solis et al. (1988)
Capra hircus	Goat	422	Lachica and Aguilera (2003)
Capra hircus	Goat (hot environment)	408	Silanikove (1986)
Madoqua saltiana phillipsi	Phillip's dikdik	404 (MR: 403 ± 51)	present study

Ovis aries	Sheep	390-447	NRC (2007)
Ovis aries	Sheep	374	Aguilera et al. (1986)
Ovis aries	Sheep	315	Vermorel et al. (1987)

Table 3

Body mass (BM) and basal metabolic rates (BMR) of selected African bovid species ordered by BM (adapted from McNab, 2008).

Species	Common name	BM (kg)	BMR (kJ kg $BM^{-0.75}$ d^{-1})	BMR (kJ h^{-1})	BMR expected from Kleibers equation (kJ h^{-1})	BMR ratio measured / expected	Climate
Madoqua saltiana phillipsi	Phillip's dikdik	2.0 ± 0.2	244 ± 39[a]	20.2	20.4	1.00	xeric
Philantomba monticola	Blue duiker	4.4	300.1	38.0	37.1	1.02	xeric
Raphicerus campestris	Steenbok	8.5	316.8	65.7	60.8	1.08	xeric
Gazella subgutturosa	Goitered gazelle	17.1	263.6	92.4	102.7	0.90	desert
Oryx leucoryx	Arabian oryx	84.1	323.4	374.2	339.1	1.10	desert
Kobus ellipsiprymnus	Waterbuck	100	406.9	536.1	386.1	1.39	mesic
Connochaetus taurinus	Blue wildebeest	140	331.5	562.2	496.9	1.12	xeric
Taurotragus oryx	Eland	150	404.8	722.9	523.3	1.38	xeric

[a]data from present study, representing resting metabolic rate